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13. ABSTRACT (Maximum 200 words) The effects of sustained stress on performance of a task to obtain food were determined. Rats were continuously exposed to a sustained avoidance/escape procedure (SAE) in which rats were exposed to signalled shock avoidance/escape trials at approximately 5 min intervals. Shock could be avoided or escaped by pulling a ceiling chain. Food was generally available by a single leverpress during most of the experiment. However, a demand curve for food was introduced either after 3 days of SAE or after 21 days of SAE. The demand curve required increasingly effortful performance by requiring 1, 5, 10, 20, 40, 80, 160 and finally 320 presses per pellet delivered on successive days. Stress alone, as expected, decreased leverpressing when only 1 press/pellet was required, especially during the first few days of the SAE procedure. However, SAE rats defended their food intake at least as strongly as controls during the demand curve portion of the experiment (i.e. increased leverpressing to try to maintain constant food delivery).			
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Effects of Sustained Avoidance/Escape on Demand for Food¹

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ELSMORE, T. F., G. J. KANT AND R. A. BAUMAN. *Effects of sustained avoidance/escape on demand for food*. *PHYSIOL BEHAV* 49(3) 621-624, 1991. —Rats were concurrently exposed to a sustained avoidance/escape (SAE) procedure and a procedure for assessing demand for food. In the sustained SAE procedure, signalled shock avoidance/escape trials were presented at varying intervals averaging five minutes. The shock could be avoided by pulling on a ceiling chain early in the trial, or escaped by pulling on the chain later in the trial. Demand curves for food were generated by requiring 1, 5, 10, 20, 40, 80, 160, and 320 lever presses for each food pellet on successive days. The demand curve procedure was introduced after either brief (3 or 5 days) or extended (21 or 23 days) exposure to SAE. Following brief exposure to SAE, SAE animals showed decreased food intake and less elasticity of demand relative to non-SAE controls. Following extended exposure to SAE, these effects were diminished or absent.

Stress Chronic stress Avoidance Escape Economics Feeding Circadian rhythms Rats

SINCE sustained performance under aversive conditions is considered to be stressful for humans, and stress is a factor in the etiology of many disease states, it is important to clearly understand the biochemical and behavioral consequences of exposure to aversive environments. Thus animal models that permit continuous monitoring of behavior during exposure to aversive environments should be useful in the investigation of stress. Previous work in our laboratories has demonstrated that performance of rats can be maintained on a sustained shock avoidance/escape (SAE) procedure for periods up to one month (2,8). This procedure produces numerous physiological changes characteristic of stress, including impaired weight gain, adrenal hypertrophy, thymus involution, and increased plasma levels of the stress-responsive hormone corticosterone.

Behavioral indicators of stress in SAE animals have been strikingly absent. Observationally, after several weeks of exposure to SAE, animals appear to be quite normal, that is, the animals continue to groom, feed, and maintain efficient SAE performance until the experiment is terminated. Food intake does decrease in animals exposed to the SAE procedure, particularly during the first few days it is in effect, recovering somewhat as the procedure is continued. After several weeks of SAE, there is little difference in food intake between SAE animals and control animals (2). In these studies, a single 45 mg food pellet was continuously available for a single press on a lever within the experimental chamber. Under these relatively simple conditions, the amount of effort required to obtain food is minimal.

It is possible that differences between experimental and control animals might be revealed if the effort to obtain food were greater. This has been dubbed the "work effect" (3). This effect

was demonstrated in a study in which pigeons received food for pecking at a key that alternated between white and red, each color being associated with a different probability of producing food. When only a single peck was required to produce food (FR 1), there were no differences in latency of pecks on the different colored keys. However, when 16 pecks were required (FR 16), large differences emerged. Thus the increased response requirement unmasked the effects of the differential reinforcement probabilities associated with the two key colors (5). Effects of this nature have recently been characterized by Hursh (7) and others as essentially economic in nature.

In an economic framework, *demand* for a commodity is measured by two variables, *level of demand*, or absolute amount of the commodity consumed, and *elasticity of demand*, which is the degree to which consumption of the commodity changes when challenged in some manner, such as an increase in response cost. As indicated earlier, the level of demand for food is decreased, at least transiently, by SAE. In the present experiment, effects of SAE on elasticity of demand were examined by changing the cost of food. This was accomplished by varying the ratio of responses to food pellets from FR 1 to FR 320 (11). To assess independence between SAE's effects on level and elasticity of demand, this manipulation was carried out both early (day 3 or day 5) or late (day 21 or day 23) after the introduction of SAE.

METHOD

Subjects

Thirty-two male albino rats purchased from Zivic Miller served

¹In conducting the research described in this report, the investigators adhered to the "Guide for the Care and Use of Laboratory Animals," as promulgated by the Committee on Care and Use of Laboratory Animals of the Institute of Laboratory Animal Resources, National Research Council. The views of the authors do not purport to reflect the position of the Department of the Army or the Department of Defense (para 4-3, AR 360-5).

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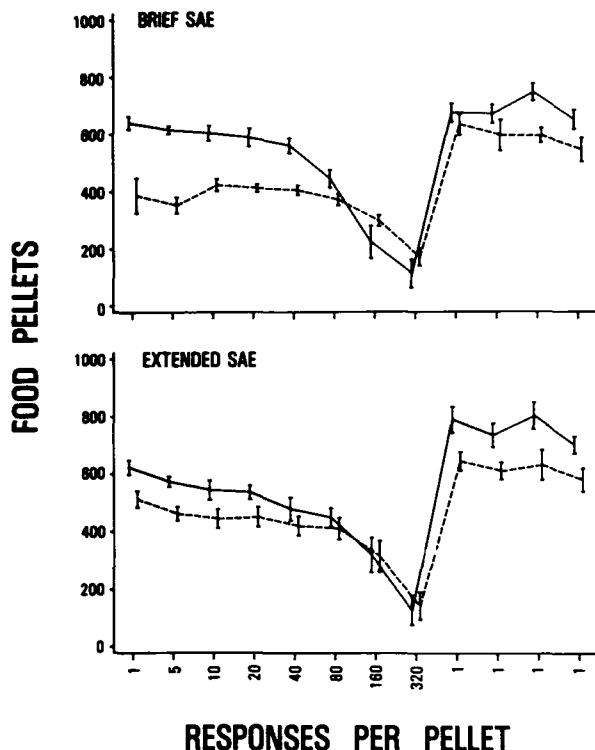


FIG. 1. Pellets consumed per day as a function of the number of lever presses required on successive days for each pellet. Each point represents the mean of eight animals \pm standard error. Solid lines are for control animals and dashed lines are for animals exposed to the SAE procedure. In the top frame, the FR was increased to 5 on either day 3 or day 5 of the SAE procedure, and in the bottom frame, the FR increases began on either day 21 or day 23 of the SAE procedure.

as subjects. Eight animals were run at a time for a total of four experiments. The range of rat weights (g) at the beginning of each of the experiments were: Experiment 1, 224–241; Experiment 2, 244–285; Experiment 3, 293–328; Experiment 4, 371–405. Each rat lived in an experimental chamber for the duration of the experiment and had continuous access to water from a bottle mounted in the cage.

Apparatus

Eight Plexiglas experimental chambers were housed in individual isolation boxes (Coulbourn Instruments). A single response lever was mounted on the aluminum front panel of the chamber to the left of a food hopper into which 45 mg food pellets (Bio-Serv) could be delivered. A triple cue lamp assembly (Coulbourn Instruments) was mounted above the lever. A chain terminating in a 5 cm diameter metal ring was hung from a microswitch mounted above the center of the ceiling such that the bottom of the ring was 10 cm above the floor. The floor was composed of 16, 0.6 cm diameter stainless steel rods spaced 1.8 cm center-to-center. The floor could be electrified with scrambled electric shock from a programmable shocker (Coulbourn Instruments, model E13-10). A fluorescent houselight was mounted inside the isolation box, outside the experimental chamber. All experimental conditions and data collection were accomplished with a PDPI1 computer using the SKED11 operating system (12). Eight rats were run at a time. For the duration of the experiment, the rats

lived in the experimental chambers. Water was available ad lib from a bottle mounted on the front panel on the opposite side from the lever. The houselight was on for 12 hours each day, starting at 0600 h.

Procedure

The general procedure was a modification of one that has been in use in our laboratory for several years (1, 2, 8). The animals were not food deprived when they were placed in the experimental chamber with food pellets available for a single lever press (FR 1). After about three days, which was sufficient time for the acquisition of lever pressing, half (4) of the animals were exposed to a continuous shock avoidance/escape (SAE) procedure in which a pull on the ceiling chain was required to terminate a SAE trial. The SAE trials consisted of a sequence of seven 5-s intervals. In the first interval, the lights over the lever were illuminated. In the second, a 4.5 kHz tone sounded. In the final 5 intervals, the tone and lights remained on, and increasing intensities of footshock were presented in the sequence 0.16, 0.32, 0.65, 1.30, and 2.60 mA. Chain pulling was shaped by manually presenting trials at irregular intervals, and manually terminating the shock contingent on successive approximations to the terminal response. When an animal had successfully terminated about five successive trials, trials were scheduled to occur randomly with an average intertrial interval (ITI) of 1 min. After an animal had terminated 35 trials, the average ITI was changed to 5 min. If at any time an animal failed to respond on 20 successive SAE trials, the ITI was reduced to 1 min until 35 avoidance/escape responses had again been made. As a safety precaution, if an animal failed to respond for a second consecutive 20 trials, the shock procedure was terminated. The program maintained a running record of the percentage of trials upon which responses occurred. When an animal had responded on 18 of the last 20 trials, 10% of the trials were made inescapable. That is, chain pulls were ineffective on 10% of the trials. This basic SAE procedure remained in effect during both the light and dark phases of the day for the duration of the experiment.

The present experiments investigated interactions between the SAE procedure and increases in food FR using a procedure for the rapid generation of curves describing demand for food (10). Four different experiments were run, with four SAE animals and four control animals in each experiment. In the first two experiments, the animals were given extended exposure to SAE prior to FR increases (21 and 23 days). In the second two experiments, the animals were given much briefer exposures to SAE (3 or 5 days) before food FR increases. On the first day of FR increases, the FR was raised to 5. On subsequent days, the FR was doubled each day (10, 20, 40, 80, 160, 320). Control animals were exposed to the same sequence of food FR's as the SAE animals. Increases in food FR were made at 0600 h, at which time the houselights were turned on. Following the FR 320 day, the FR was reduced to 1, and 4 recovery days were allowed before the animals were removed from the experimental chambers.

RESULTS

All data to be presented are taken from the eight sessions beginning with the last day before the FR was increased to 5, through the FR 320 day, and for four recovery FR 1 days. Table 1 shows the mean pellets consumed by each group on each FR for all conditions of the experiment. There were no statistically significant differences between replications for the brief SAE condition, so data from the two replications were pooled for analysis. There were, however, some differences between runs for the extended

TABLE 1
MEAN PELLETS PER DAY UNDER DIFFERENT FR
REQUIREMENTS \pm S.E.M.

FR	Replication 1		Replication 2	
	NS	S	NS	S
Brief SAE Exposure				
1	60.2 \pm 22.8	385.7 \pm 61.5	605.7 \pm 96.5	359.5 \pm 44.5
5	101.5 \pm 24.8	379.5 \pm 43.2	628.0 \pm 13.7	324.5 \pm 36.9
10	563.5 \pm 40.5	449.2 \pm 34.2	643.7 \pm 25.1	395.7 \pm 22.0
20	556.5 \pm 41.0	413.0 \pm 19.0	620.0 \pm 49.9	409.5 \pm 21.8
40	506.0 \pm 22.0	414.5 \pm 13.1	611.5 \pm 30.8	392.5 \pm 33.1
80	400.7 \pm 50.6	383.5 \pm 41.7	484.5 \pm 30.2	356.5 \pm 11.1
160	201.7 \pm 95.9	315.5 \pm 17.7	243.2 \pm 77.3	277.0 \pm 35.4
320	145.2 \pm 83.9	166.7 \pm 39.1	81.0 \pm 62.2	173.0 \pm 52.5
Extended SAE Exposure				
1	579.7 \pm 13.9	487.2 \pm 26.6	666.0 \pm 40.3	535.2 \pm 54.0
5	536.7 \pm 18.6	434.5 \pm 10.0	608.0 \pm 19.9	487.2 \pm 47.2
10	465.7 \pm 18.6	376.0 \pm 32.3	620.5 \pm 34.7	512.2 \pm 31.5
20	485.5 \pm 17.9	404.5 \pm 64.0	584.7 \pm 29.7	495.7 \pm 17.2
40	385.7 \pm 32.6	343.2 \pm 21.8	568.7 \pm 34.0	494.5 \pm 32.9
80	421.7 \pm 29.5	390.5 \pm 58.3	474.5 \pm 61.1	429.2 \pm 56.6
160	316.2 \pm 80.2	329.5 \pm 67.7	321.5 \pm 03.5	299.0 \pm 95.7
320	118.0 \pm 82.3	160.5 \pm 56.4	138.7 \pm 73.9	126.7 \pm 86.1

Each value represents the mean \pm the s.e.m for four animals.
S and NS designate Shock and No-Shock groups respectively.

exposure conditions, so the data were analyzed separately. Statistical analyses were performed with the SAS general linear models procedure.

SAE Effects on Baseline Food Intake

The effects of the SAE procedure on food intake are illustrated in Fig. 1 in which pellet intake is plotted against the number of responses required to earn each pellet. Solid lines are from the control (nonshocked, NS) groups, and dashed lines are from the shocked (S) groups. The top frame shows that following a brief exposure to the SAE procedure there was a significant difference in food intake under FR 1 between the S and NS groups with the S group consuming only about 60% of the NS group's intake, $F(3,15)=5.67$, $p<0.02$. There was also a significant difference between S and NS groups under FR 1 following extended exposure to the SAE procedure (bottom frame), $F(3,15)=4.24$, $p<0.05$, but the difference was considerably smaller with the S group consuming about 82% of the NS group's total. Food intake in the NS groups was comparable in both experiments, $F(1,15)=0.97$, with the NS groups in the brief and extended conditions consuming about 620 pellets per day, but significantly less following brief exposure to the SAE procedure than following extended exposure [372 vs. 511 respectively, $F(1,15)=8.54$, $p<0.02$], indicating recovery of food intake with extended exposure to SAE.

Interactions Between SAE and Response Cost

In all cases, increasing the FR for food decreased total daily food intake. The curves of Fig. 1 show that as FR was increased, the NS group intakes were higher than the S groups until 160 lever presses were required to obtain each pellet. At FR's of 160

TABLE 2
MEAN PERCENT PELLETS EARNED IN THE DARK PHASE OF THE
LIGHT/DARK CYCLE UNDER DIFFERENT FR REQUIREMENTS

FR	Replication 1		Replication 2	
	NS	S	NS	S
Brief SAE Exposure				
1	88.4 \pm 2.1	90.6 \pm 5.3	92.5 \pm 3.4	84.0 \pm 3.3
5	97.3 \pm 1.3	82.7 \pm 3.7	84.1 \pm 2.7	89.6 \pm 4.0
10	92.3 \pm 2.4	93.8 \pm 3.5	96.7 \pm 1.9	89.9 \pm 4.4
20	99.4 \pm 0.1	92.7 \pm 3.0	92.5 \pm 3.5	94.7 \pm 2.3
40	97.7 \pm 1.3	95.9 \pm 3.8	93.8 \pm 2.9	90.8 \pm 4.5
80	98.9 \pm 0.3	96.7 \pm 1.0	95.9 \pm 2.1	98.8 \pm 0.6
160	72.3 \pm 4.1	98.0 \pm 0.9	94.4 \pm 3.7	85.2 \pm 0.7
320	91.0 \pm 5.8	97.2 \pm 2.0	87.9 \pm 9.3	98.4 \pm 0.9
Extended SAE Exposure				
1	80.7 \pm 2.0	76.6 \pm 5.1	86.4 \pm 2.8	77.5 \pm 3.8
5	82.3 \pm 2.6	70.5 \pm 8.4	82.7 \pm 5.1	76.9 \pm 2.1
10	79.9 \pm 1.5	84.7 \pm 5.1	87.8 \pm 3.8	84.5 \pm 2.1
20	89.1 \pm 3.7	78.7 \pm 4.1	75.1 \pm 2.1	89.0 \pm 2.5
40	81.9 \pm 3.1	86.6 \pm 7.3	87.1 \pm 3.6	85.5 \pm 2.2
80	92.9 \pm 2.8	77.2 \pm 2.5	77.5 \pm 0.5	77.7 \pm 3.8
160	91.4 \pm 3.4	92.7 \pm 4.9	92.6 \pm 2.2	84.5 \pm 2.9
320	93.2 \pm 3.4	81.1 \pm 3.4	79.0 \pm 2.8	79.8 \pm 3.67

Each value represents the mean \pm the s.e.m for four animals.
S and NS designate Shock and No-Shock groups respectively.

and 320, intakes were higher for the S groups. Two-way analyses of variance (group \times FR) were conducted for the eight days beginning with the last day of FR 1 through FR 320. For the brief exposure condition, significant effects were found for group, FR, and the group \times FR interaction ($p<0.0001$ in all cases). There were significant differences between the replications following extended exposure, so separate analyses were conducted for both replications. In both cases, there were significant effects for group ($p<0.05$, $p<0.02$, for the first and second replications), and FR ($p<0.0001$, for both replications). However, unlike the situation following brief exposure to the SAE procedure, there was no interaction between group and FR in either replication.

SAE Effects on Circadian Rhythms

In an attempt to further characterize the differences between the two conditions, we analyzed the distribution of food intake across the day. Table 2 shows the percentage of pellets earned in the dark phase of the light/dark cycle. As expected, all rats lever-pressed more for food during the dark. In all cases, the effect of FR was highly significant ($p<0.001$), but there were no significant differences between groups or group by FR interactions.

Recovery Effects

All groups showed a rebound in food intake after the FR was again decreased to 1. When food intake on the first recovery day was compared with food intake on the last day of FR 1 prior to the FR increases, intake of the shock groups was significantly above baseline [brief SAE, $F(1,15)=16.86$, $p<0.002$; extended SAE, $F(1,15)=34.65$, $p<0.0001$]. Figure 1 shows that following this initial rebound, all groups showed a trend back towards baseline.

DISCUSSION

In the present experiment, exposure to SAE reduced the absolute level of demand for food. Following about three weeks of exposure to the SAE procedure, the difference between SAE animals and controls was considerably less, although it was still statistically significant. Although leverpressing for food in the SAE animal was less than controls on FR 1, the elasticity of demand for food in SAE animals was less than that of controls when the cost of food was increased after the first 3–5 days of exposure to SAE. That is, food intake relative to that during FR 1 decreased less in animals concurrently exposed to the SAE procedure than in animals only working for food. When animals were allowed to adapt to the SAE procedure for about three weeks, this effect was no longer apparent.

The reduced elasticity of demand observed in the brief exposure condition was somewhat surprising, since our initial assumption was that the FR increases would exacerbate the stress of the SAE procedure. There are several possible explanations for these differences in elasticity.

One explanation is based on differences in "stressfulness" of the FR increases in SAE animals relative to the NS animals. The aversiveness of large FR's has been repeatedly demonstrated. For example, animals will work to escape from a stimulus associated with large FR's (13), stimuli associated with large FR's can suppress behavior when delivered as a consequence of that behavior (14), and stimuli associated with large FR's reliably elicit aggression in pigeons (4,6). However, it is difficult to see how the FR

increases could be more aversive or stressful in the NS groups than in the S groups.

It is possible that the relative aversiveness of the FR increase was less in the S animals than in the NS animals, since they were already being exposed to the SAE procedure, thus the added stress of the large food FR's may have been less significant, thus producing a smaller effect on elasticity of demand for food. When the FR increases were introduced after extended exposure to SAE, when the animals were presumably less stressed, the relative increase in aversiveness of the higher food FR's was possibly greater, resulting in smaller differences between the S and NS groups.

The SAE procedure required the animals to respond consistently throughout the day, whereas the control animals typically slept during the lights-on half of the 24-hour cycle. Thus it might be argued that since they were up anyway, the SAE animals had more time to eat, thus their food intake declined less when the FR was increased. However, as Table 2 shows, there were no differences between the groups in the effects of FR increases on nocturnality of feeding, with all groups behaving in a similar fashion.

The most likely explanation appears to be economic in nature. As we showed, a prominent effect of SAE was to reduce food intake prior to the increase in FR. Thus the SAE animals were more food deprived, leading to greater strength of food-maintained responding, as shown by their greater resistance to change when the cost of food was increased. In cost-benefit terms, each increase in FR in the SAE rats was effectively a smaller increase than a similar increase in control rats [cf. (8)].

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